

Estimation of Demographic Parameters from Live-Encounter Data: a Summary Review

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Abstract

Estimation of demographic parameters is central to research questions in wildlife management, conservation, and evolutionary ecology. I review the 7 major classes of mark-recapture models that investigators can use to estimate apparent survival and other parameters from live-encounter data. Return rates are the product of 4 probabilities: true survival (S), site fidelity (F), site propensity (δ), and true detection (p^). Cormack-Jolly-Seber (CJS) models improve upon return rates by separating apparent survival ($\phi = S \times F$) from the probability of encounter ($p = \delta \times p^*$). The main drawback to mark-recapture models based on live-encounter data is that the complement of apparent survival ($1 - \phi$) includes losses to mortality and to permanent emigration, and these 2 ecological processes are difficult to disentangle. Advanced mark-recapture models require additional sampling effort but estimate apparent survival with greater precision and less bias, and they also offer estimates of other useful demographic parameters. Time-since-marking or transient models control for individuals not encountered after the occasion they are first marked, a common feature of wildlife populations. Temporal symmetry models combine forward- and reverse-time modeling to estimate recruitment (f) and the finite rate of population change (λ). Multi-strata models include dynamic categorical information and offer state-specific estimates of apparent survival and encounter rates, as well as probabilities of changing states (Ψ). Robust design models subdivide sampling occasions into shorter periods, and they partition encounter rates (p) into estimates of temporary emigration ($\gamma = 1 - \delta$) and true detection (p^*). Joint models combine live encounters with other sources of information, including dead-recovery data, and decompose apparent survival into estimates of true survival (S) and site fidelity (F). Cormack-Jolly-Seber and multi-strata models have a large literature, but many of the advanced models have not yet received widespread use. In the future, wildlife ecologists should design field studies that take advantage of the best possible statistical procedures now that a range of alternative models and software tools are available. (JOURNAL OF WILDLIFE MANAGEMENT 70(6):1504–1520; 2006)*

Key words

apparent survival, Cormack-Jolly-Seber, joint model, multi-strata, population change, recruitment, return rate, robust design, temporal symmetry, transient.

Estimates of fecundity, survival, and the age-specific variation in these demographic parameters often guide management and conservation decisions for wildlife populations. Fecundity rates are widely used because reproductive output is relatively easy to measure by direct counts of offspring number if the probability of breeding is high. Survival rates can be more informative but are challenging to estimate under field conditions because the timing and causes of mortality are usually unknown for free-living animals (Lebreton et al. 1992). Moreover, investigators rarely know the number of age (or stage) classes with unique combinations of demographic rates unless they have conducted long-term monitoring of known-aged individuals. Nevertheless, if age-specific estimates of fecundity and survival are available, investigators can use population models based on projection matrices to explore the sensitivity of the finite rate of population change (λ) to changes in different demographic parameters (Caswell 2001).

Survival is only a single component of population change, but analyses based on projection matrices frequently identify survival as the demographic parameter with the greatest potential impact on λ (Crone 2001). In long-lived species and declining populations, survival rates of the oldest age class or largest stage class frequently have the highest elasticity value (Heppell 1998, Heppell et al. 2000, Sæther

and Bakke 2000). On the other hand, survival of juveniles may have the highest elasticity value in short-lived species and growing populations (Wisdom and Mills 1997, Haydon et al. 1999, Blomberg and Shine 2001, Sandercock et al. 2005a). High elasticity values imply that management actions affecting survival rates will have the greatest potential to modify rates of population change, even if low variance in survival or logistical considerations favor interventions that target other vital rates.

Estimation of survival rates and other demographic parameters for wildlife populations requires 1 of 4 types of data: age ratios, radiotelemetry, dead recoveries, or live encounters. Age ratios are estimated from the standing age distribution of a population or by tracking cohorts of individuals through time. Calculating survival from age distributions requires that 3 restrictive assumptions are met: the population must have a stable age distribution, the rate of population change must be stationary, and different age classes must have an equal probability of encounter (Williams et al. 2002). If a sample contains 2 age classes, then adult survival (\hat{S}_a) is calculated as: $(\hat{S}_a) = \hat{A}/(\hat{Y} + \hat{A})$, where \hat{A} and \hat{Y} = the estimated number of adults and yearlings in the sample. If a sample contains multiple age classes, then investigators can use life-table methods. The survival rate of a particular age class (S_x or p_x) is estimated from the number of individuals in 2 consecutive age classes as: $\hat{S}_x = \hat{l}_{x+1}/\hat{l}_x$, where \hat{l}_x is the estimated number of individuals surviving x years after birth. Use of age

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distributions may be the only option under certain conditions, such as analysis of specimens in natural history collections (Ricklefs 1997, Rohwer 2004). However, age distributions have less value for field studies of wildlife populations because violations of the underlying assumptions are likely to lead to biased estimates of survival (Kelly and Finch 2000, Conn et al. 2005, but see Ricklefs and Rohwer 2005).

Radiotelemetry is a key tool for monitoring wildlife species, and investigators can conduct survival analyses based on telemetry data with a range of different statistical procedures (Williams et al. 2002). The drawbacks to telemetry for estimation of annual survival rates for wildlife populations are mainly practical considerations. The current battery life, size, and range of conventional and satellite transmitters prohibit monitoring of small-bodied species of migratory animals throughout their annual cycle. Transmitters are more intrusive than individual tags, and attachment techniques should not affect demographic rates (Hagen et al. 2006, Mong and Sandercock 2007). Radiotelemetry is an expensive technology and the financial costs of transmitters and tracking effort restrict the number of individuals that investigators can monitor in a population study.

Dead recoveries and live encounters of individually marked animals have been widely used to estimate survival rates for wildlife species. Dead-recovery data require that observers locate and report individually marked animals after harvest or natural death. Among North American birds, the proportion of bands recovered (\hat{f}) is adequate for hunted species of waterfowl (median $\hat{f} = 0.135$, $n = 35$ spp.; Franklin et al. 2002) but dismal for nongame species of shorebirds (0.014, $n = 28$; Wilcox 1959) and songbirds (0.004, $n = 225$; Francis 1995). Recovery models may have greater utility for European birds because established ringing programs have marked larger samples of birds over longer periods of time and reporting rates seem to be higher (Paradis et al. 1998, Piersma et al. 2005).

While alternative sources of information have their merits, live-encounter data often remain the only feasible method for estimating annual survival rates for nongame species of wildlife. Statistical methods for analysis of live-encounter data have advanced greatly in recent years, with development of new mark-recapture models (Williams et al. 2002), new model-selection procedures based on information theory (Burnham and Anderson 1998, Johnson and Omland 2004, Stephens et al. 2005), and new software tools (White and Burnham 1999). The goals of this article are: 1) to present a summary review of the 7 major classes of open-population mark-recapture models that investigators can use to estimate demographic parameters from live-encounter data, 2) to discuss potential advantages and drawbacks of these 7 models, and 3) to highlight empirical applications where these models have been applied to wildlife populations under field conditions.

I defined the scope of this article in 4 ways. First, mark-recapture models for live-encounter data are primarily used

to estimate survival and abundance (Caswell and Fujiwara 2004), but I consider their utility for estimation of other demographic parameters as well. Second, I focus on open population models for estimation of transition probabilities, but note that closed population models have other advantages for analyses of live-encounter data. Third, I emphasize estimation of annual rates, but investigators can use mark-recapture models to estimate parameters for a variety of time intervals. Fourth, I discuss applications to wildlife populations, but investigators can also apply mark-recapture models for live-encounter data to plants (Shefferson et al. 2003, Kéry and Gregg 2004), insects (Auckland et al. 2004), fish (Labonne and Gaudin 2005), and other organisms. A final caution is that the notation for demographic parameters in mark-recapture models has not been standardized. Investigators have used alternative symbols to denote the same parameter (e.g., site fidelity: F or η ; seniority: ζ or γ) and the same symbol to denote separate parameters in different mark-recapture models (e.g., τ : site propensity or transience; γ : temporary emigration or seniority). In my notation, I followed conventions of the published literature but avoided use of identical symbols for parameters from different models.

Return Rates

One metric that commonly is used as an index of annual survival for wildlife populations is the return rate, the proportion of marked individuals marked in a year of sampling that are recaptured the following year or in some block of future years. The probability of capturing an individual animal in 2 consecutive years at a single sampling site is the product of 4 separate probabilities:

- 1) True survival (S): the probability that an individual survives between 2 sampling periods.
- 2) Site fidelity (F): the probability that an individual returns to the same sampling area and does not permanently emigrate, if it is still alive (with probability S).
- 3) Site propensity (δ): the probability that an individual is available for encounter in the same sampling area the next year, if it is alive (with probability S) and in the sampling area (with probability F).
- 4) True detection (p^*): the probability that an observer detects the individual under field conditions, given that the individual is alive (with probability S), in the sampling area (with probability F), and available for encounter (with probability δ).

As the product of these 4 probabilities ($rr = S \times F \times \delta \times p^*$), return rates (rr) are a minimum estimate of true survival. If return rates are high ($rr > 0.8$), then true survival and each of the other 3 probabilities must be higher still. Difficulties arise in the interpretation of low or moderate return rates ($rr < 0.6$) and in comparisons of variation in return rates among different groups or years. A low return rate ($rr = 0.4$) could be the result of poor survival ($rr = 0.55 \times 0.9 \times 0.9 \times 0.9 = 0.4$), weak site fidelity ($rr = 0.9 \times 0.55 \times 0.9 \times 0.9 = 0.4$), or any other possible combination of the 4

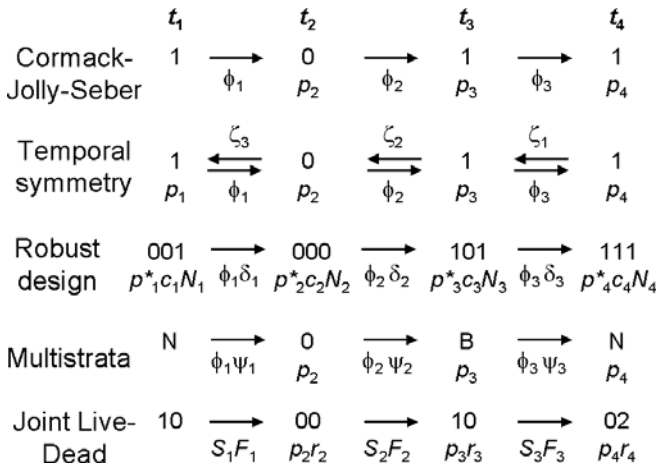


Figure 1. A comparison of encounter histories and mark-recapture models for analyses of live-encounter data. The example contains 4 occasions (t_1 to t_4) and 3 intervals (arrows). In Cormack-Jolly-Seber, temporal symmetry, and robust design models, encounters at each occasion (L or LLL) are coded as: 1 = detected and 0 = not detected. In the multi-strata model, detections are coded as categorical states such as: B = breeding, and N = nonbreeding. In the joint live-dead model, detections at each occasion (LD) are coded as: 1 = detected alive, and 2 = recovered dead. Demographic parameters that can be estimated from live-encounter data include the probabilities of apparent survival (ϕ), encounter (p), seniority (ζ), true detection (p^*), recapture (c), population size (N), site propensity (δ), changing strata (ψ), true survival (S), site fidelity (F) and reporting (r).

parameters. Return rates are a negatively biased estimate of true survival if any of the 3 other probabilities are <1 (Martin et al. 1995). Negative bias should have greater consequences for management of long-lived animals if adult survival has a high elasticity value.

Given the expected problems of bias and interpretation, investigators should avoid return rates if possible. However, return rates may be the only estimator available if the duration of a project is 2–3 years. Return rates can be used as a relative index of true survival but only if investigators are willing to make assumptions about the remaining 3 probabilities. If one assumes that site fidelity, site propensity, and true detection are equivalent among groups, then differences in return rates can be ascribed to variation in true survival. Similarly, it is possible to compare temporal trends in return rates among 2 or more locations if one assumes that the distributions of a subset of the probabilities are stationary, if not equivalent.

Jolly-Seber and Cormack-Jolly-Seber Models

The first step in any mark-recapture analysis is to assemble encounter histories for all uniquely marked individuals. In standard mark-recapture models for open populations, each sampling occasion is coded as: 1 = an observer detected the individual, or 0 = an observer did not encounter the individual (Fig. 1). In live-encounter data, detections of uniquely marked individuals may include physical captures, resightings, or both. If inspection of the encounter histories reveals gaps where observers did not detect some individuals in intervening years (e.g., 1011), then the probability of

encounter is <1 . Next, investigators select the factors that will be included in the set of candidate models a priori, they apply goodness-of-fit procedures to the most general starting (or global) model to determine whether a variance inflation factor (\hat{c}) is needed to correct for possible overdispersion, and then use model selection procedures to identify parsimonious models for parameter estimation (Burnham and Anderson 1998).

The Jolly-Seber (JS) model estimates 4 parameters from the encounter histories: the probability of apparent (or local) survival ($\phi = S \times F$), the probability of encounter ($p = \delta \times \hat{p}^*$), population size (N), and the number of new individuals entering the population (B ; Pollock et al. 1990). Unfortunately, individual heterogeneity and other issues often lead to bias in estimates of N and B from JS models. Thus, analyses of live-encounter data frequently rely on the Cormack-Jolly-Seber (CJS) model, a restricted model that estimates 2 of the 4 parameters: apparent survival (ϕ) and the probability of encounter (p ; Lebreton et al. 1992). Standard CJS models usually contain group (grp) or time-dependence (t) and may be denoted $\phi_{grp \times t}$ $p_{grp \times t}$ where the \times indicates an interaction between the categorical factors. Cormack-Jolly-Seber models have been widely applied to a diverse range of wildlife populations, including amphibians (Anholt et al. 2003), reptiles (Freilich et al. 2000, Willemsen and Hailey 2001), birds (Sandercock and Gratto-Trevor 1997, Rivera-Milán and Schaffner 2002, Morrison et al. 2004, Ward et al. 2004), and mammals (Langtimm et al. 1998, Lindenmayer et al. 1998).

One limitation of CJS models is that ϕ and p are both products of multiple parameters. If modeling of a set of encounter histories indicates that $p = 1$, then return rates are equivalent to apparent survival ($rr = \phi$) and can be analyzed with logistic regression. This situation is unusual but does apply to some stage classes (breeders: Cam and Monnat 2000, Sandercock et al. 2000, Robertson et al. 2006; territory holders: Johnson et al. 2001) and to some populations (McElligott et al. 2002, Ozgul et al. 2004). If $p < 1$, but true detection rates are assumed to be stationary, investigators can use encounter rates as a relative index of site propensity ($p \approx \delta$; Cooch et al. 2001).

In general, ϕ will be a less-biased estimator of true survival than return rates because the effects of variation in δ and \hat{p}^* have been removed. Similar to return rates, estimates of ϕ will be high if S and F are both high (e.g., $\hat{\phi} > 0.93$, puffins [*Fratercula arctica*]: Breton et al. 2005; murrees [*Uria aalge*]: Robertson et al. 2006). Cormack-Jolly-Seber models estimate true survival ($\phi = S$) for sessile animals with limited movements because site fidelity is likely to be high ($F = 1$, Vilella et al. 2004). Conversely, CJS models can be used to estimate site fidelity ($\phi = F$) if true survival rates are high during a short-term study ($S = 1$, Boulanger and McLellan 2001, Schaub et al. 2001). In open population models for most vagile animals, however, the complement of apparent survival ($1 - \phi$) will include losses to mortality and to permanent emigration, and the relative importance of

these 2 ecological processes is difficult to disentangle if ϕ is low ($\hat{\phi} < 0.6$).

An inability to separate S from F is a general feature of all mark-recapture models based solely on live-encounter data and is the single greatest drawback to estimating survivorship from this source of information. Terminology frequently obscures this issue. In a seminal monograph, Lebreton et al. (1992) defined ϕ as survival, and this practice has continued (e.g., Cam et al. 1998, Flint et al. 2000, Jones et al. 2002, Ward et al. 2004). The risk in denoting ϕ as survival and not apparent survival is that ϕ may be misunderstood to be true survival, and the possibility that variation in ϕ is due to differences in site fidelity may be overlooked. In practice, mark-recapture models based on live-encounter data may have limited utility for estimating demographic rates for animals that have low site fidelity, such as species that utilize unstable habitats (Haig and Oring 1988) or ephemeral food resources (Senar et al. 1993, Blake and Loiselle 2002). Live-encounter data are also problematic for estimating juvenile survival if the natal dispersal distances of juveniles are greater than the breeding dispersal movements of older age classes (Paradis et al. 1998, Blums et al. 2003, Sandercock et al. 2005b).

In any analysis based on live-encounter data, investigators should consider variation in both S and F when interpreting estimates of ϕ . One ad hoc approach is to present independent data on dispersal distances alongside estimates of ϕ . For example, Sandercock and Gratto-Trevor (1997) found that female semipalmated sandpipers (*Calidris pusilla*) had lower apparent survival than males ($\phi_f = 0.56$ vs. $\phi_m = 0.61$). They attributed sex differences in ϕ to variation in site fidelity because females dispersed farther to mate with new partners in this male-territorial species (174 m vs. 46 m). To evaluate the potential effects of $F < 1$, other investigators have modeled apparent survival as a function of distance to edge of the study area or separately for individuals marked in a core study area but also resighted in a surrounding buffer zone (Powell et al. 2000, Boulanger and McLellan 2001, Cilimburg et al. 2002, Marshall et al. 2004). Unfortunately, use of dispersal distances or distance to edge of a study plot is an incomplete solution because the size and configuration of a study area places an upper limit on the maximum detectable dispersal distance (Baker et al. 1995, Koenig et al. 1996). Both ϕ and dispersal distance are underestimated when dispersal movements lead to permanent emigration. For example, Stenzel et al. (1994) documented snowy plovers (*Charadrius alexandrinus*) moving up to 1,140 km between consecutive nesting attempts within the same breeding season. It is unlikely that any study plot or buffer zone will be large enough to accurately measure either ϕ or dispersal distances from live-encounter data for wildlife species with extensive dispersal movements.

A final consideration in use of CJS and other mark-recapture models for live-encounter data is the duration of the study. At least 3 years of information are necessary to obtain a single estimate of p . With time-dependence in both ϕ and p , it is not possible to estimate p for the last sampling

occasion. Thus, ϕ and p cannot be estimated separately for the last interval in a time series and the product of the 2 transition rates becomes a parameter of the model ($\beta = \phi p$). Thus, n years of study would yield $n - 2$ estimates of apparent survival, and longer time-series are necessary to model apparent survival as a function of annual variation in environmental conditions.

Time-Since-Marking and Transient Models

A common feature of live-encounter data is that observers may fail to detect a subset of the sample of marked individuals after the first capture occasion. If encounter histories with captures on only a single occasion comprise a large portion of a sample (e.g., 1000, 0100), the apparent survival rates of newly marked individuals in the interval immediately after first capture (ϕ^1) will be lower than the apparent survival of previously marked individuals in subsequent intervals (ϕ^{2+}). In a sample of animals marked as young, ϕ^1 may be less than ϕ^{2+} if age-specific variation is present in either S or F . In a sample of animals marked as adults, ϕ^1 may still be less than ϕ^{2+} if relative age or capture and handling affect S or F , if capture rates are heterogeneous, or if observers unintentionally include transient individuals that are moving through a sampling area (Pradel et al. 1995, 1997a, Sedinger et al. 1997, Prévot-Julliard et al. 1998, Sandercock and Jaramillo 2002). Distinguishing among these nonexclusive alternatives is a major challenge in most field studies. Nevertheless, ϕ^{2+} will be a less-biased estimate of true survival whenever $\phi^1 < \phi^{2+}$ because ϕ^1 and ϕ^{2+} are pooled in standard CJS models with only group- or time-dependence (Johnston et al. 1997).

Time-since-marking and transient models are both types of CJS models that control for individuals not detected after the first capture occasion. Encounter histories for both models are coded in the same manner as for standard CJS models (Fig. 1), but a more complex model structure estimates additional parameters. In time-since-marking models, ϕ^1 and ϕ^{2+} are estimated separately, along with the encounter rate (p). These models can be denoted $\phi_{2ac \times t}$, p_t (where $2ac = 2$ age classes) or as $\phi_t^1, \phi_t^{2+}, p_t$. If applied to a sample of known-aged individuals, an age model describes this model structure. "Time-since-marking" is a more appropriate term, however, because investigators can apply the same model structure to a sample of unknown age. Investigators also can apply time-since-marking models to encounter rates to investigate the short-term effects of trap-dependence (e.g., ϕ_t, p_t^1, p_t^{2+}), but they must first modify the encounter histories (Pradel 1993, Doligez et al. 2004).

Studies of wildlife populations frequently have selected models with 2 or more age classes as the best fit for apparent survival: common toads (*Bufo bufo*; Schmidt et al. 2002), grouse (3 spp.; Hagen et al. 2005, Sandercock et al. 2005a), migratory geese (2 spp.; Francis and Cooke 1993, Pradel et al. 1995, Reed et al. 1998), breeding seabirds (5 spp.; Prévot-Julliard et al. 1998, Fredericksen and Petersen 1999, Bertram et al. 2000, Jones et al. 2002), shorebirds (7 spp.; Sandercock 2003, Sandercock et al. 2005b), ruby-throated

hummingbirds (*Archilochus colubris*; Hilton and Miller 2003), songbirds (19 spp.; Johnston et al. 1997, Blake and Loiselle 2002, Cilimburg et al. 2002, Sandercock and Jaramillo 2002, Dugger et al. 2004), rodents (3 spp.; Lambin and Yoccoz 1998, Julliard et al. 1999, Kraus et al. 2005), pipistrelle bats (*Pipistrellus pipistrellus*; Sendor and Simon 2003), seals (2 spp.; McMahon et al. 2003, Jessopp et al. 2004), and ungulates (5 spp.; Loison et al. 1999). A general finding of these studies is that apparent survival rates are usually ranked: juveniles after first capture < adults after first capture < adults in subsequent intervals.

In the special case where failure to encounter individuals after first marking likely is due to permanent emigration by transients, investigators can employ alternative methods. Some investigators have handled transience by developing a residency index based on the number of captures within a sampling occasion. Individuals captured once may be discarded or grouped as transients, whereas individuals captured 2 or more times are grouped as residents (Chase et al. 1997, Ward et al. 1997, Bayne and Hobson 2002, Cilimburg et al. 2002, Morrison et al. 2004, Ozgul et al. 2004). This approach can be efficient if encounter rates are high, but a potential drawback is that observers may misclassify residents if they are captured only once. Transient models improve upon ad hoc approaches to dealing with transience by using a modified version of the time-since-marking models. The proportion of transients among unmarked individuals (τ_t) at time t is estimated as $\hat{\tau}_t = 1 - \hat{\phi}_t^1 / \hat{\phi}_t^{2+}$, and τ_t appears as a term in the model notation (τ_t, ϕ_t, p_t ; Pradel et al. 1997a). One potential pitfall of transient models is to misinterpret τ_t as the proportion of the entire population that are transient. The parameter τ_t applies to newly marked individuals only, and the proportion of transients among this subset of the population can be estimated as $T_t = \hat{\tau}_t N_t / (N_t + m_t)$, where N_t and m_t are the numbers of newly marked and recaptured individuals at time t (Jessopp et al. 2004). Estimation of the proportion of transients relative to the entire population is possible but requires a modified modeling approach (Oro et al. 2004).

Empirical applications of the transient model have shown that a high proportion of transients may be a general feature of animal populations, including alpine newts (*Triturus alpestris*, $\hat{\tau} = 0.43\text{--}0.48$; Perret et al. 2003) and loggerhead sea turtles (*Caretta caretta*, $\hat{\tau} = 0.19\text{--}0.68$; Chaloupka and Limpus 2002). In birds, transients are a feature of Swainson's thrushes (*Catharus ustulatus*, $\hat{\tau} = 0.56$; Rosenberg et al. 1999), and other migrant songbirds captured at stopover sites (8 spp., $\hat{\tau} = 0.49\text{--}0.79$; DeSante et al. 1995). Investigators also have detected transients in at least 6 populations of resident landbirds, including black-capped chickadees (*Poecile atricapillus*, $\hat{\tau} = 0.27$; Loery et al. 1997), serins (*Serinus serinus*; $\hat{\tau} = 0.47\text{--}0.80$; Conroy et al. 1999), Eurasian blackbirds (*Turdus merula*; $\hat{\tau} = 0.57$; Miller et al. 2003), and other songbirds (3 spp., $\hat{\tau} = 0.34\text{--}0.58$; DeSante et al. 1995; 7 spp., $\hat{\tau} = 0.04\text{--}0.68$; Nott and DeSante 2002), and in 2 populations of colonial birds, including Audouin's gull (*Larus audouinii*, $\hat{\tau} = 0.08\text{--}0.14$; Oro et al. 1999) and

cliff swallows (*Petrochelidon pyrrhonota*, τ not reported; Brown and Brown 2004). Comparisons of parameter estimates show that standard CJS models underestimate apparent survival if the proportion of transients is large (DeSante et al. 1995, Loery et al. 1997, Rosenberg et al. 1999, Chaloupka and Limpus 2002).

Overall, empirical applications of time-since-marking and transient models indicate that individuals not detected after the first capture occasion are a common feature of mark-recapture data for many wildlife populations. The ecological processes creating such encounter histories may be difficult to determine, but a prudent approach to analysis of CJS encounter histories would be to include time-since-marking or transience in any starting global model. If time-since-marking models receive little support, investigators can always discard these candidate models later (e.g., Sandercock and Gratto-Trevor 1997, Sandercock et al. 2000). Where standard CJS models require 3 years of data, investigators need at least 4 years to estimate the extra parameters of the time-since-marking and transient models.

Temporal Symmetry Models

Encounter histories for temporal symmetry models are coded in the same format as CJS models (Fig. 1). Temporal symmetry models differ from standard CJS models in that investigators analyze the encounter histories simultaneously with both forward and reverse-time modeling (Pradel 1996, Franklin 2001, Nichols and Hines 2002). Forward-time modeling yields the usual estimates of apparent survival (ϕ) and encounter rates (p). Reverse-time modeling of the same encounter histories from the last capture backwards yields a seniority probability (ζ), defined as the probability that an individual did not enter the population between the previous and current occasion. Forward-time modeling assumes homogeneous capture probabilities among marked animals, but reverse-time modeling extends this assumption to both marked and unmarked individuals, a more difficult restriction to meet (Nichols et al. 2000). In the recruitment or f -parameterization of the temporal symmetry model (ϕ_t, p_t, f_t), the parameters ϕ and ζ are combined to estimate the per capita rate of recruitment $\hat{f}_t = \hat{\phi}_t(1 - \hat{\zeta}_{t+1}) / \hat{\zeta}_{t+1}$. In the λ -parameterization (ϕ_t, p_t, λ_t), the same 2 parameters are used to estimate the finite rate of population change $\hat{\lambda}_t = \hat{\phi}_t / \hat{\zeta}_{t+1}$.

Most available estimates of population change are based upon deterministic matrix models ($\hat{\lambda}_p$), and estimates from temporal symmetry models ($\hat{\lambda}_r$) are a new development. When selecting a modeling approach, it is important to recognize that $\hat{\lambda}_p$ and $\hat{\lambda}_r$ have markedly different properties (Sandercock and Beissinger 2002). Where $\hat{\lambda}_p$ is the predicted rate of change if a population is exposed to the same set of demographic rates for an indefinite period, $\hat{\lambda}_r$ is a realized estimate of population change in past intervals. Moreover, $\hat{\lambda}_p$ is a mathematical expectation that integrates across all age or stage classes in the matrix model, whereas $\hat{\lambda}_r$ is the rate of population change for the single age class included in the encounter histories (usually adults, Ozgul et al. 2006). If a population is at the stable age distribution, all age classes

should increase at the same rate, and estimates of $\hat{\lambda}_r$ for adults may be extrapolated to the entire population. Investigators should apply temporal symmetry models with caution if age-specific variation in fecundity and survival is likely to be complex, or if deviations from stable age distributions are expected. Direct comparisons of $\hat{\lambda}_p$ and $\hat{\lambda}_r$ are somewhat inappropriate, but Sandercock and Beissinger (2002) found that field estimates of $\hat{\lambda}$ from the 2 types of models were comparable for at least one bird population.

Temporal symmetry models offer at least 3 advantages. First, temporal symmetry models permit direct estimation of λ without requiring a complete census of the population or estimation of all the demographic rates needed to parameterize a matrix model. Thus, investigators can use estimates of $\hat{\lambda}_r$ to assess population trajectory even if abundance is unknown. These features are particularly helpful when working with species of conservation concern where demographic data may be limited. Second, $\hat{\lambda}_r$ explicitly includes gains from immigration, which have been included in only a few matrix models for wildlife populations (Cooch et al. 2001, Sandercock and Beissinger 2002, Webb et al. 2002). Without inclusion of immigrants, $\hat{\lambda}_p$ may underestimate the expected rate of population change (Franklin et al. 2004). Last, seniority parameters are analogous to elasticity values from matrix models because investigators can use ζ to identify important components of $\hat{\lambda}$ (Nichols et al. 2000). Survival has a greater effect on $\hat{\lambda}_r$ if $\zeta > 0.5$, recruitment has a greater effect on $\hat{\lambda}_r$ if $\zeta < 0.5$, and the 2 demographic processes have equal influence if $\zeta = 0.5$.

Empirical applications of temporal symmetry models are few. A few studies have used reverse-time modeling alone to investigate factors affecting recruitment in populations of birds (Pradel et al. 1997b, Cooch et al. 1999, Oro and Pradel 2000, Cam et al. 2005). Investigators have used the f -parameterization of the temporal symmetry models to explore factors affecting recruitment in freshwater mussels (3 spp.; Vilella et al. 2004), snakes (2 spp.; Webb et al. 2002), and small mammals (2 spp.; Lima et al. 2003). Other studies have used the λ -parameterization to obtain direct estimates of $\hat{\lambda}$ for diamondback terrapins (*Malaclemys terrapin*; Mitro 2003), white-winged scoters (*Melanitta fusca*; Alisauskas et al. 2004), marbled murrelets (*Brachyramphus marmoratus*; Cam et al. 2003), raptorial birds ([*Rostrhamus sociabilis*] Dreitz et al. 2002; [*Strix occidentalis occidentalis*] Franklin et al. 2004), green-rumped parrotlets (*Forpus passerinus*; Sandercock and Beissinger 2002), ruby-throated hummingbirds (Hilton and Miller 2003), songbirds (4 spp.; Julliard 2004), and yellow-bellied marmots (*Marmota flaviventris*; Ozgul et al. 2006). At least 4 of the above studies have reported both ϕ and ζ : hummingbirds had low apparent survival and seniority values ($\hat{\phi} < 0.43$ and $\hat{\zeta} = 0.36$), scoters had intermediate values ($\hat{\phi} = 0.81$ and $\hat{\zeta} = 0.83$), and terrapins and murrelets had high values ($\hat{\phi} > 0.92$ and $\hat{\zeta} > 0.84$). In the latter 2 species, high seniority values indicate that survival had >5 times of an effect on $\hat{\lambda}$ than recruitment. This sample of studies is limited, but the variation in seniority values is consistent with interspecific

comparisons of matrix models where elasticity of adult survival tends to be high in long-lived species (Heppell 1998, Heppell et al. 2000, Sæther and Bakke 2000).

Temporal symmetry models have 4 potential drawbacks (Franklin 2001, Hines and Nichols 2002, Nichols and Hines 2002). First, they usually require long time series of data. Time-dependence in both ϕ and p leads to inestimable terms in both the first and last intervals of the study period ($\beta = \phi p$), and n occasions would yield $n - 3$ estimates of $\hat{\lambda}$. For example, a 4-year study of snail kites yielded a single estimate of $\hat{\lambda}$ (Dreitz et al. 2002). Second, temporal symmetry models are sensitive to changes in sampling area. Contraction and expansion of the boundaries of a study site lead to losses and gains of marked individuals that temporal symmetry models treat as changes in population size. Third, behavioral responses to trapping, heterogeneity of capture, and failure to account for losses at capture are likely to bias λ (Hines and Nichols 2002). Last, temporal symmetry models work well for a population without age-structure, but reverse-time modeling becomes more complex if a sample includes individuals marked as young and as adults. At present, there is no straightforward approach for handling age-structure in temporal symmetry models, although a combined reverse-time and robust design model (Ramsey 2005) or a combined robust design and multi-strata model (Nichols et al. 2000) may be viable options.

Robust Design Models

Robust design models are similar to CJS models in that the encounter histories are coded with 1 = detected and 0 = not encountered. Robust design models differ from CJS models in that investigators must subdivide primary sampling periods into shorter secondary sampling periods (Fig. 1). Robust design models assume that populations are open between primary sampling periods but closed within secondary sampling periods (Kendall and Nichols 1995, Kendall et al. 1997), which permits estimation of temporary emigration from a sampling area (Schaub et al. 2004). A key assumption of this model is that the survival rates are the same for individuals inside and outside of the sampling area. Robust design models perform well under some violations of the closure assumption (Kendall 1999), and recent formulations relax the assumption of closure to allow staggered entry and exit of individuals from the sampling area within primary periods (Schwarz and Stobo 1997, Kendall and Bjorkland 2001, Bailey et al. 2004a, Kendall 2004).

In the CJS model, the probability of encounter (p) is the product of site propensity (δ) and the true probability of detection (p^*). In the robust design model, p^* is estimated from the closed population data in the secondary samples, along with the probability of recapture (c) and population size (N). If the closed portion of the model reveals that $\hat{p}^* = 1$, then encounter rates are effectively an estimate of site propensity ($\hat{p} = \hat{\delta}$; Anderson et al. 2001). In the case of random temporary emigration, investigators use closed population statistics to estimate \hat{p}_t^* and open population statistics to estimate \hat{p}_t and calculate the probability of

temporary emigration (i.e., $\gamma = 1 - \delta$) as $\hat{\gamma}_t = 1 - \hat{p}_t / \hat{p}_t^*$. In the case of nonrandom (or Markovian) temporary emigration, the probability of temporary emigration at time t is modeled as a function of an individual's status in the previous occasion ($t - 1$). Thus, robust design models estimate γ separately for individuals that were absent and remain absent (γ_t') and individuals that were present but have temporarily emigrated from the sampling area (γ_t'' ; Kendall et al. 1997). The parameter γ_t' is sometimes described as an immigration parameter, but the probability that an absent individual re-enters the sampling area should be calculated as the complement: $\hat{\delta}_t' = 1 - \hat{\gamma}_t'$. Investigators also have used robust design models to examine trap response at time t among individuals that were not trapped (γ_t) or trapped (γ_t') at $t - 1$ (Kendall and Nichols 1995), and to estimate recruitment from in situ reproduction versus immigration as the number of adults in the population at time t that were young at $t - 1$ (B_{t-1}') or entered the population as adults between $t - 1$ and t (B_{t-1}'' ; Nichols and Pollock 1990).

Robust design models have at least 3 advantages. First, the closed portion of robust design models makes it possible to obtain robust estimates of abundance, which may be of interest to wildlife managers. Second, if time-dependence is present in the demographic parameters, robust design models may offer parameter estimates for more intervals than CJS or temporal symmetry models. The closed portion of the model allows estimation of γ and p^* for all occasions; thus, it is always possible to estimate ϕ for the first and last intervals of a time series. Third, robust design models can yield estimates of ϕ and p with less bias and greater precision than CJS models. Temporary emigration causes heterogeneity in encounter rates because individuals with site propensity have a $p^* > 0$, whereas $p^* = 0$ for emigrants. Under random temporary emigration, estimates of ϕ and p from CJS models are relatively unbiased, but a reduction in precision occurs (Kendall et al. 1997). Under nonrandom temporary emigration, estimates of ϕ and p from standard CJS models often are strongly biased, both when $\gamma_t' > \gamma_t''$ and when $\gamma_t' < \gamma_t''$ (Kendall et al. 1997, Fujiwara and Caswell 2002).

One important application of robust design models has been to investigate temporary emigration in wildlife populations (Schaub et al. 2004). Temporary emigration is a poorly understood demographic process that may be a common feature of many wildlife populations. Individuals marked as young at traditional breeding or wintering locations may temporarily emigrate from such sites and return to the sampling area after a delay of several years (Fujiwara and Caswell 2002). Similarly, individuals marked as adults will be temporary emigrants if they skip a breeding opportunity (Viallefont et al. 1995, Kendall and Bjorkland 2001, Schmidt et al. 2002) or if they temporarily move to a site where they are not available for capture (Hestbeck et al. 1991, Dinsmore et al. 2003). Marked individuals also can be temporary emigrants if they remain in the sampling area but are unavailable for capture. This will be the case whenever

animals are inactive or dormant in belowground refugia (Schaub and Vaterlaus-Schlegel 2001, Bailey et al. 2004b, Villella et al. 2004).

Robust design models have provided many of the first empirical estimates of temporary emigration. For example, Bailey et al. (2004b) found that *Plethodon* salamanders had high rates of temporary emigration ($\hat{\gamma} = 0.87$) because a substantial proportion of the population were belowground and unavailable for capture. Similarly, male boreal toads (*Bufo boreas*) have moderate rates of temporary emigration from breeding ponds at high-elevation sites ($\hat{\gamma}' \approx \hat{\gamma}'' = 0.07$ – 0.55 ; Muths et al. 2006). Dinsmore et al. (2003) reported low rates of temporary emigration ($\hat{\gamma}'' \approx 0.23$) among mountain plovers (*Charadrius montanus*) moving out of their sampling area. Last, Kendall et al. (1997) showed that the probability of temporary emigration in white-footed mice (*Peromyscus leucopus*) was highest (grid 1: $\hat{\gamma}'$ and $\hat{\gamma}'' > 0.39$, grid 2: $\hat{\gamma} > 0.72$) during sampling periods when climatic conditions were cold and mice were inactive in burrows.

Robust design models also have provided some of the first estimates of age-specific variation in breeding propensity. Breeding propensity is an essential component of matrix models because investigators should calculate fecundity rates as the product of both the probability of breeding and the number of offspring produced per breeder. A conventional assumption in many matrix models is that the probability of breeding is 0 among immature or subadult age classes, and it becomes 1 once an individual attains the age at maturity. Empirical applications of robust design models show that the probability of breeding may increase with age as a step function in wildlife populations, increasing from $\hat{\delta} = 0.67$ among 2- to 3-year-olds to $\hat{\delta} = 0.90$ among 5⁺-year-old female black brant (*Branta bernicla*; Sедinger et al. 2001), and reaching a maximum at 7 years in grey seals (*Halichoerus grypus*; Schwarz and Stobo 1997). Robust design models also have revealed that the conditional probability of breeding can be < 1 among mature adults: $\hat{\delta}' = 0.53$ – 0.61 in common toads (Schmidt et al. 2002), $\hat{\delta}' = 0.34$ – 0.80 in hawksbill sea turtles (*Eretmochelys imbricata*; Kendall and Bjorkland 2001), and $\hat{\delta} = 0.57$ in snow geese (*Chen caerulescens*; Reed et al. 2004).

A final application of robust design models has been to explore population dynamics by partitioning recruitment rates into gains from local reproduction and immigration by adults. At least 4 studies have used this approach to estimate recruitment: a study of snow geese (Cooch et al. 2001) and 3 studies of small mammals. Population gains from local reproduction were greater than gains from immigration ($B_{t-1}' > B_{t-1}''$) in meadow voles (*Microtus pennsylvanicus*; Nichols and Pollock 1990) and house mice (*Mus musculus*; Pocock et al. 2004), but the opposite was true in red-backed voles (*Clethrionomys rutilus*; McDonough and Rexstad 2005).

One hurdle for field applications of the robust design model is that investigators must subdivide sampling effort in primary periods into shorter secondary periods. Such

sampling designs may require additional effort to ensure an adequate number of encounters within each secondary period. A second problem is that marking schemes for some wildlife species may violate the assumptions of the robust design. If estimation of survival rates is primarily based upon dead-recovery information, investigators may actively avoid recaptures of previously marked individuals to ensure that the number of newly marked individuals released each year is maximized. In a study of arctic-nesting snow geese, such a sampling design prevented use of robust design models for estimation of breeding propensity (Cooch et al. 2001).

New hybrid models have combined robust design methods with other approaches, including the transient (Hines et al. 2003), reverse-time (Ramsey 2005), multi-strata (Kendall et al. 2003), and joint information models (Barker et al. 2004). Nott and DeSante (2002) applied the robust design-transient model to mark-recapture data from breeding songbirds and obtained estimates of apparent survival that had greater precision compared to estimates from a transient-only model ($\Delta CV(\hat{\phi}) = 1.3\text{--}29.3\%$, $n = 8$ spp.). Last, Ramsey (2005) used a combined robust design-reverse-time model to successfully separate the contributions of fecundity, immigration, and survival to population growth rates for 3 age classes of brushtail possums (*Trichosurus vulpecula*).

Multi-Strata Models

Multi-strata (or multi-state) models are similar to CJS models in that investigators do not subdivide primary sampling occasions into shorter secondary periods. They differ from CJS models because they permit inclusion of categorical data or 'strata' in the encounter histories that can change during the life span of an individual (Brownie et al. 1993, Lebreton and Pradel 2002). For a multi-strata model, an encounter history could be coded as $A = \text{site A}$ and $B = \text{site B}$, instead of $1 = \text{detected}$ as in the CJS models (Fig. 1). As in CJS models, $0 = \text{not encountered}$. The main advantage of multi-strata models is that they yield estimates of apparent survival (ϕ_i^A and ϕ_i^B) and encounter rates (p_i^A and p_i^B) that are specific to each categorical state. Multi-strata models also yield estimates of the probabilities of changing states, such as movement rates of individuals from site A to site B (ψ_i^{A-B}) or in the opposite direction (ψ_i^{B-A}).

In the standard Arnason-Schwarz (or first-order Markovian) multi-strata model, the separation of apparent survival into strata-specific estimates (r) of apparent survival and movement ($\phi_r = \phi_i^r \psi_i^r$) requires that 2 assumptions are met: apparent survival in the interval between time i to $i + 1$ does not depend on the stratum at time $i - 1$, and all individuals make the transition at the end of the interval (Brownie et al. 1993). Two additional assumptions are that observers correctly assign individuals to strata on each occasion, and that no individuals temporarily emigrate to strata where encounters do not occur (Kendall 2004). These 4 assumptions can be relaxed in memory (or higher-order Markovian) models that model transition probabilities as a function of

strata occupied on previous occasions (Hestbeck et al. 1991, Brownie et al. 1993), in cases where the distribution of transition times is known (Joe and Pollock 2002), and in modified models that account for uncertainty or include temporary emigrants as an unobservable state (see below).

One use of multi-strata models has been to test hypotheses about apparent survival and movements where breeding populations are subdivided into discrete geographic sites due to nesting on islands (Spendelov et al. 1995, Cam et al. 2004), colonial breeding (Lindberg et al. 1998, Brown et al. 2003, Grosbois and Tavecchia 2003, Drake and Alisauskas 2004, Serrano et al. 2005), or habitat fragmentation (Lens et al. 2002, Senar et al. 2002, Barbraud et al. 2003). Investigators also have applied multi-strata models in situations where the habitat is subdivided but patches are contiguous (Hestbeck et al. 1991, Murphy 2001, Béchet et al. 2003, Pettorelli et al. 2003, Auckland et al. 2004). These studies have shown that ϕ and ψ can be affected by spatial variation in size and proximity of colonies (Spendelov et al. 1995, Lens et al. 2002, Brown et al. 2003, Serrano et al. 2005), habitat quality (Senar et al. 2002, Pettorelli et al. 2003), and hunting activity (Béchet et al. 2003), as well as temporal variation in resource abundance (Auckland et al. 2004) and climatic conditions (Hestbeck et al. 1991).

Grosbois and Tavecchia (2003) extended standard multi-strata models by partitioning the transition rates (e.g., ψ_i^{A-B}) into a 2-stage process of movement: the probability that an individual departs from one site (π_i^A), and the probability that the individual then settles into a different site (μ_i^{A-B}). The $\pi\mu$ parameterization requires minor modification of the encounter histories and currently is limited to situations with up to 3 sites but will likely provide additional insights into animal movements. Multi-strata models based on spatial information are particularly useful because estimates of movement rates can be used to parameterize spatially implicit metapopulation models for modeling the dynamics of subdivided populations.

Investigators also have used multi-strata models to investigate the effects of social status (Cam et al. 1998, Sandercock et al. 2000, Scofield et al. 2001, McGowan et al. 2003, Barbraud and Weimerskirch 2005) and age on demographic rates (Wood et al. 1998, Cam and Monnat 2000, Coffman et al. 2001, Blums et al. 2003, Ozgul et al. 2004, Cam et al. 2005). In these situations, encounter histories are coded by social status ($B = \text{breeder}$, $N = \text{nonbreeder}$) or by age class ($J = \text{Juvenile}$, $A = \text{Adult}$), and $0 = \text{not detected}$. The 2 rates ϕ and p are estimated separately for each demographic group, and the transition rate ψ becomes an estimate of the probability of changing social status or the probability of maturation. If experience or age are ordinal variables that progress during maturation, then the probability of regression to inexperienced or younger strata is usually fixed to zero.

Multi-strata models based on social status for green-rumped parrotlets and 3 species of seabirds found that breeders had higher apparent survival, were more likely to remain breeders, and had higher encounter rates than

nonbreeders (Cam et al. 1998, Sandercock et al. 2000, Scofield et al. 2001, Barbraud and Weimerskirch 2005). In prairie voles (*Microtus ochrogaster*), adults had higher apparent survival rates than juveniles, and males had higher rates of maturation than females (Ozgul et al. 2004). If both age and site are included as states, then multi-strata models offer age-specific estimates of the probability of changing sites (Blums et al. 2003, Lebreton et al. 2003). Social status and age are sources of heterogeneity that would be pooled in a standard CJS model but can be examined separately in multi-strata models.

Multi-strata models are particularly flexible for modeling live-encounter data because investigators can consider a broad range of categorical variables. In addition to the factors above, studies have used multi-strata models to investigate covariates describing individual quality: natural or manipulated clutch size (Viallefont et al. 1995, Doligez et al. 2002), number of breeding attempts (Johannesen et al. 2003), body mass or fat reserves (Bradshaw et al. 2003, Miller et al. 2003), social group affiliations (Traylor et al. 2004), and disease state (Faustino et al. 2004, Senar and Conroy 2004). In the latter 2 studies, infected individuals (*I*) had lower apparent survival rates than uninfected individuals (*U*), and transition rates provided estimates of disease dynamics (infection: ψ^{U-I} , recovery: ψ^{I-U}). Similarly, Johnson (2005) examined the spatial dynamics of sylvatic plague in black-tailed prairie dogs (*Cynomys ludovicianus*) by creating encounter histories for colonies instead of individuals.

At least 3 studies have used variants of multi-strata models to investigate the effects of neck collars on arctic-nesting geese (Alisauskas and Lindberg 2002, Conn et al. 2004, Reed et al. 2005). A key assumption of mark-recapture methods is that marking techniques have no effect on subsequent survival, and investigators tested this assumption by marking geese with either leg bands only (*L*) or a combination of leg and neckbands (*N*). In some cases, neck-banded geese had lower apparent survival or encounter rates, and multi-strata models provided an estimate of the probability of neckband loss (ψ^{N-L}).

One challenge in multi-strata modeling arises when observers cannot directly monitor individuals in one or more strata (Lebreton et al. 2003, Kendall 2004). If unobservable states are due to temporary emigration, then multi-strata models provide a useful alternative to robust design models for estimation of breeding propensity (Bailey et al. 2004a, Schaub et al. 2004). In a multi-strata model, the 2 states might be coded as *O* = observable and *U* = unobservable. The movement parameters of a multi-strata model with an unobservable state are then analogous to the estimates of temporary emigration from a nonrandom robust design model: the probability that an absent individual remains absent is ψ_i^{U-U} or γ_i' , whereas the probability that an individual that was present temporarily emigrates from the sampling area is ψ_i^{O-U} or γ_i'' (Kendall et al. 1997, Kendall and Nichols 2002). In the robust design model, investigators estimate the probability of detection for observable states with closed population models by sampling

in the secondary periods. In multi-strata models, estimation of transition rates for observable and unobservable states is only possible if investigators impose constraints upon a subset of the parameters to eliminate problems with parameter identifiability (Fujiwara and Caswell 2002, Kendall and Nichols 2002).

At least 4 studies have attempted to model unobservable strata by applying constraints to multi-strata models. In most studies that have investigated social status with multi-strata models, breeders and nonbreeders are both observable and the 2 strata are included in the encounter histories. In North Atlantic right whales (*Eubalaena glacialis*) and snow geese, however, nonbreeders are an unobservable segment of the population that fail to migrate to breeding areas where sampling of animals occurs (Fujiwara and Caswell 2002, Reed et al. 2003). In both cases, the authors solved problems with parameter identifiability by setting apparent survival rates to be equal for the observable and unobservable strata. A similar situation arises in studies of the demography of perennial plants where ramets occur in 3 states: unobservable rhizomes that are dormant below ground and observable vegetative and flowering shoots (Shefferson et al. 2003, Kéry and Gregg 2004). In this case, estimation with multi-strata models is made possible by fixing the strata-specific encounter rates (rhizomes: $p^D = 0$, shoots: $p^V = p^F = 1$). By applying constraints to p , it was possible to estimate true survival and transition rates for all 3 ramet strata even though investigators did not directly monitor the below-ground life-stage.

Another challenge in multi-strata modeling arises when observers cannot assign an individual to a categorical state with certainty (Kendall 2004, Nichols et al. 2004, Senar and Conroy 2004). Three approaches to dealing with uncertain strata include: use of ancillary information to estimate the expected frequency of different states (e.g., sex ratio; Sandercock et al. 2005b), discarding all observations or encounter histories that include uncertain states (Cam et al. 1998), or defining incomplete information as an additional unknown state (Wood et al. 1998, Conroy et al. 1999, Faustino et al. 2004). Two studies have used numerical simulations to explore the effects that removing unknown observations or including this information as an additional state has upon the parameter estimates of the multi-strata model (Faustino et al. 2004, Nichols et al. 2004). Apparent survival was relatively unbiased if unknown observations were included or removed, transition probabilities (ψ) were biased only if unknowns were included, but encounter rates were biased low in both cases, particularly if the percentage of unknown observations was relatively high ($\geq 25\%$).

Kendall et al. (2003) addressed the problem of uncertain strata by combining the multi-strata model with the robust design model. Observers recorded the breeding status of female Florida manatees (*Trichechus manatus*) during 2 secondary sampling periods nested within each primary sampling occasion. The combined model controlled for misclassification errors and estimated the transitional probability of becoming a breeder to be $\hat{\phi}^{N-B} = 0.61$,

whereas the same parameter was underestimated as $\hat{\phi}^{N-B} = 0.31$ with a standard multi-strata model. Combined multi-strata and robust design models have been used by Bailey et al. (2004a) and Skvarla et al. (2004) to estimate demographic parameters for tiger salamanders (*Ambystoma tigrinum*) and banner-tailed kangaroo rats (*Dipodomys spectabilis*), respectively.

Nichols et al. (2004) dealt with uncertainty in sex determination by developing a modified multi-strata model for 2 sampling scenarios. Investigators construct encounter histories for uncertain-strata models by either treating every capture occasion as an independent attempt to assign strata, or by assuming that strata assignments do not change once they have been determined. The uncertain-strata model yields the usual estimates of apparent survival and encounter rates, but also estimates a classification parameter (δ), the strata-specific probability that an individual is classified with certainty, and a mixture parameter (π), the probability that an unmarked individual belongs to one of the known strata. Transition rates (ψ) are not estimated. This model provided some of the first sex-specific estimates of apparent survival for roseate terns (*Sterna dougallii*), a species of conservation concern where the sexes are difficult to distinguish in all age classes.

One past concern for multi-strata models was the lack of a reliable test for assessing fit of a global model, but new goodness-of-fit procedures (Pradel et al. 2003, 2005) and accompanying software are now available (Program U-Care; Choquet et al. 2003). The main limitation of multi-strata models is that the number of parameters (K) to be estimated increases rapidly if investigators include a large number of categorical states in the encounter histories or if they use memory models. Complex multi-strata models may require substantial amounts of data and adequate computer resources for fitting the log-likelihood function. Thus, multi-strata models are usually restricted to a maximum of 2–4 states. For example, Brown et al. (2003) observed colonies of sociable weavers (*Philetairus socius*) that ranged from <2–>500 individuals, but they reduced this variation to 3 categories to model the effects of colony size on apparent survival. Similarly, Drake and Alisauskas (2004) marked a large sample of Ross's geese ($n = 3,233$ adults [*Chen rossii*]), and attempted to model ϕ , ψ , and p as a function of colony (5 levels), sex (2), and year (4 intervals). They did not detect inter-colony movements for 99 of 160 possible transitions in a 5-strata model, and they collapsed the number of colony strata from 5 to 3 before proceeding with further analyses.

Joint Models for Combined Sources of Information

Joint models combine live-encounter data with either radiotelemetry or dead-recovery information. Investigators can use joint models to estimate survival with greater precision, and to estimate other useful demographic parameters as well. Multi-strata models are one possible approach for combining different sources of information

(Lebreton et al. 1999, Williams et al. 2002), and investigators have used multi-strata models to combine information from banded and radiotagged wood thrushes (*Hylocichla mustelina*; Powell et al. 2000), hair samples of unmarked and radiomarked grizzly bears (*Ursus arctos*; Boulanger et al. 2004), and live-encounter and dead-recovery data from multiple sites (Kendall et al. 2006). In the first 2 studies, the authors treated different marker types as separate groups and the core and peripheral regions of a study site as strata in the encounter histories. They then used multi-strata models to estimate movement rates and the marker-specific values of ϕ and p .

Investigators have developed specialized models for joint analysis of live-encounter and radiotelemetry data (Nasution et al. 2001, 2004) and live-encounter and dead-recovery data (Burnham 1993, Barker 1997, 1999). In the Burnham and Barker models, encounter histories have one value for each type of information per occasion (i.e., LD format; Fig. 1). Live encounters usually are taken from a small sampling area, but dead recoveries are reported from a much larger geographic region, which reduces losses to permanent emigration. Thus, one major advantage of joint models based on live encounters and dead recoveries is that apparent survival can be decomposed into the probabilities of true survival (S) and site fidelity (F).

The Burnham model estimates 4 parameters: S , F , and the probabilities of capture (p) and reporting (r) for live and dead animals, respectively (Fig. 1). Lindberg et al. (2001) extended the Burnham model by placing it in a robust design framework. In addition to S , F , p , and r , the closed population elements of this model allow estimation of 3 other parameters: the probability of recapture (c), and the conditional probabilities of temporary emigration (γ' and γ''). The Barker model combines encounter data from 3 separate sources: live encounters, dead recoveries, and live resightings between encounter occasions. In addition to S , F , p , and r , the Barker model estimates 3 more parameters: the probabilities of live resighting (R), resighting before mortality (R'), and immigration (F'). The Barker model has also been extended to estimate demographic parameters corrected for possible tag loss (Conn et al. 2004) and for temporary emigration (Barker et al. 2004).

Investigators have mainly applied the Burnham and Barker models to hunted species of gamebirds: lesser prairie-chickens (*Tympanuchus pallidicinctus*; Hagen et al. 2006), dabbling ducks (*Anas strepera*, Szymczak and Rexstad 1991; 3 spp., Blums et al. 2002; *Anas platyrhynchos*, Doherty et al. 2002), diving ducks (*Aythya valisineria*, Lindberg et al. 2001; *Aythya americana*, Arnold et al. 2002; *Bucephala clangula*, Ludwischowski et al. 2002; 3 spp., Blums et al. 2005), sea ducks (*Melanitta nigra*; Fox et al. 2003), geese (*Chen caerulescens*, Cooch et al. 2001; *Branta* and *Anser* spp., Alisauskas and Lindberg 2002; *Branta bernicla*, Sedinger et al. 2002; *Chen rossii*, Slattery and Alisauskas 2002; *Anser* spp., Fredericksen et al. 2004), and cormorants (*Phalacrocorax carbo*; Fredericksen and Bregnballe 2000). However, applications of joint models to nongame species are growing in number. The

Burnham model has been applied to blacklip abalone (*Haliotis rubra*; Catchpole et al. 2001), turtles (3 spp.; Bjørndal et al. 2003, Fannesbeck and Dodd 2003, Seminoff et al. 2003), Eurasian golden-plovers (*Pluvialis apricaria*; Piersma et al. 2005), peregrine falcons (*Falco peregrinus*; Craig et al. 2004), owls (2 spp.; Francis and Saurola 2002, Altwegg et al. 2003), and western bluebirds (*Sialia mexicana*; Keyser et al. 2004), whereas the Barker model has been applied to little penguins (*Eudyptula minor*; Johannesen et al. 2003), peregrine falcons (Kauffman et al. 2003), Finsch's oystercatchers (*Haematopus finschi*; Sagar et al. 2002), snowy plovers (L. E. Stenzel, Point Reyes Bird Observatory, unpublished data), grey seals (Hall et al. 2001), and humpback whales (*Megaptera novaeangliae*, Mizroch et al. 2004). Joint models for live-encounter and dead-recovery data have provided some of the first robust estimates of true survival (S) and site fidelity (F) that are not confounded by other probabilities. Moreover, joint models have permitted explicit tests of the effects of age, sex, and environmental conditions upon variation in site fidelity and other demographic parameters.

The main hurdle for use of the Burnham and Barker models is that multiple sources of information for tagged animals are unlikely to be available for most wildlife populations. The 6 studies where investigators applied Barker models to nongame species are encouraging exceptions. The penguin and seal population studies were both conducted at sites where tourist operations provided opportunities to view wildlife. The remaining 4 studies were based on coordinated networks of experienced volunteers who contributed resighting data for species of conservation concern. The geographic distribution of the dead-recovery data is key to the successful application of joint models. In 2 studies, investigators recovered dead individuals in the same restricted sampling area where animals originally had been marked (Fannesbeck and Dodd 2003, Keyser et al. 2004). Although the recovery regions were small, the authors could still consider S to be an estimate of true survival because the study populations were geographically isolated. Nevertheless, if permanent emigration from the recovery region is possible, then estimates of survival from joint models are best viewed as a probability of apparent survival ϕ and not true survival S (Francis and Saurola 2002).

Management Implications

Effective management of wildlife populations requires the best possible estimates of survival and other demographic rates. Mark-recapture analyses of live-encounter data are likely to remain an important source of information, especially for nongame species. The main drawback to use of mark-recapture models for live-encounter data is that it rarely is possible to estimate true survival rates, and investigators must consider ecological factors affecting both true survival (S) and site fidelity (F) when interpreting estimates of apparent survival (ϕ) from JS and CJS models.

Empirical applications of advanced mark-recapture models are a logistical trade-off between the requirements of collecting additional information, and the potential for

obtaining a better understanding of wildlife demography. Time-since-marking models and temporal symmetry models require at least 4 years of data but are useful for controlling for transients and calculating rates of population change. Multi-strata models require inclusion of categorical states but allow calculation of transition rates for dynamic strata. Robust design models require additional sampling within sampling occasions but allow decomposition of encounter rates into site propensity and true detection rates. Similarly, joint models require multiple sources of information but allow partitioning of apparent survival into true survival and site fidelity.

Advances in analyses of live-encounter data are likely to proceed in 3 major directions: creative applications of available models, ongoing development of new models, and increased use of Bayesian approaches to model fitting. Standard CJS and multi-strata models each have a large literature, but most of the advanced models have untapped potential for addressing demographic questions in wildlife ecology. Mark-recapture methods are an exciting area of research and new models address uncertainty in state assignment (Nichols et al. 2004), combine robust design methods with other models (Lindberg et al. 2001, Hines et al. 2003, Kendall et al. 2003, Ramsey 2005), and combine the best features of multiple models (Barker and White 2004). Applications of new models may be limited by a lack of goodness-of-fit tests for assessment of over-dispersion and by data requirements if model structure is complex. Finally, most models for live-encounter data rely on maximum likelihood estimators, which are based upon a fixed-effects framework. Biometricians have developed Bayesian approaches to model fitting for a subset of mark-recapture models, including the CJS (Brooks et al. 2000), and multi-strata models (King and Brooks 2002). Bayesian methods have distinct advantages, including development of hierarchical models that treat demographic parameters as random variables (Cam et al. 2002, Royle and Link 2002, Link and Barker 2005). In the future, wildlife ecologists should design studies that take advantage of the best possible statistical procedures, now that a range of alternative models and model-fitting approaches are available for estimation of survival and other demographic parameters.

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